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Case study

Predicting the response of *Cabomba caroliniana* populations to biological control agent damage

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Abstract *Cabomba caroliniana* is a submerged aquatic plant from South America that is becoming a serious weed worldwide. It spreads by seed and by fragmentation and has an extremely wide climatic range, invading lakes and ponds from tropical (Darwin, Australia: latitude 12°) to cold temperate regions (Peterborough, Canada: latitude 45°). There are currently no effective methods of managing cabomba infestations and funding has been allocated to research biological methods. Surveys have examined cabomba in its native range and have identified several potential biological control agents. The most promising are a stem boring weevil (*Hydrotimetes natans*) and an aquatic moth (*Paracles* spp.). Here we predict the change in cabomba populations after the introduction of the biological control agents. Our predictions are based on quantitative surveys of cabomba populations at three lakes in south-east Queensland, qualitative observations of cabomba in its native range, and conceptual knowledge of how the realised niche of cabomba might be affected by herbivore damage.

Key words aquatic weeds, defoliation, herbivory, insect damage, water fanwort.

INTRODUCTION

Classical biological control is based on the concept of 'enemy release' where introduced organisms gain a competitive advantage in their new range due to a lack of specialist predators, herbivores or pathogens (Culliney 2005; but see Keane & Crawley 2002). Therefore, the introduction of a specialist natural enemy is expected to reduce the fitness of the target organism. The natural enemy will affect the populations directly, but will also reduce competitive ability and the ability of the target organism to tolerate stresses associated with disturbances and low resource abundance. Based on these concepts, knowledge of feeding habits of two potential biological control agents, and data on plant populations in Australia, we predict changes in stem length, plant density and biomass should the agents be released.

Study organism

Cabomba (*Cabomba caroliniana*: Cabombaceae), or water fanwort, is a fast-growing submerged aquatic weed that has the potential to spread throughout the aquatic habitats of Australia (Mackey & Swarbrick 1997; Ensbey 2000). It is also considered a problem weed in the USA, Canada, Greece, Japan and China. It grows well in slow-moving water bodies, particularly where nutrient concentrations are high. Cabomba prefers areas of permanent standing water less than 3 m deep and is often found along the margins of lakes and reservoirs. However, it has been found rooted at depths to 6 m (Schooler & Julien 2006). The weed is easily recognised by its finely dissected underwater leaves that are feathery or fan-like in appearance. The small white flowers (2 cm diameter) have yellow centres and are comprised of three white petals and three white sepals. They often extend above the water's surface, making weed infestations more visible during the summer months. Reproduction is almost entirely vegetative in Australia. Although some seeds and seedlings have recently been found near Darwin in the Northern Territory, seeds have not been found at any other site in Australia. Any small fragments that include the leaf nodes can grow into a new plant.

Cabomba originates from South America (Orgaard 1991). It was brought into Australia through the aquarium trade (Mackey & Swarbrick 1997). The plant's tolerance of fragmentation and ease of cultivation make it a desirable aquarium plant. Cabomba was subsequently introduced into lakes and streams both accidentally, through the dumping of aquarium water, and on purpose, to enable cultivation for later collection and sale. Currently, cabomba is primarily found in rivers and dams of coastal Queensland and New South Wales. However, isolated populations occur from near Darwin (Pine Creek and the Darwin River) to lakes north of Melbourne (Benella and Nagambie). It is easily spread across drainages on water craft, boat trailers and perhaps by waterfowl. Cabomba is a declared weed throughout Australia (it is illegal to propagate, move or sell) where it is listed as one of 20 Weeds of National Significance (WoNS).

Cabomba negatively affects the environment, recreational activities, public safety and water quality (Mackey &

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Swarbrick 1997). The weed can smother native submerged plants such as pondweeds (*Potamogeton* spp.), stoneworts (*Chara* spp.), hornwort (*Ceratophyllum demersum*) and water nymph (*Najas tenuifolia*). Cabomba may also reduce germination of desirable native emergent plants. Alteration of the flora is thought to have reduced populations of platypus and water rats in northern Queensland (Mackey & Swarbrick 1997). In southern Queensland, cabomba appears to negatively affect populations of the endangered Mary River cod (T Anderson pers. comm. 2004). The long stems of cabomba impede the movement of boats and can get tangled in propellers, paddles and fishing lines. This makes many recreational activities less desirable in areas infested with cabomba and thereby reduces tourism. In addition, cabomba is a potential danger to swimmers who may become entangled in the long stems. Cabomba also decreases water quality for human consumption by tainting and discolouring potable water supplies and therefore increases water treatment costs. It interferes with dam machinery, such as valves, pumps and aerators, which leads to increased costs of maintenance. In addition, cabomba reduces water flow in irrigation canals and blocks pumps, which increases production costs.

Currently, there is little that can be done to control cabomba once it is established (Anderson & Diatloff 1999). Herbicides are largely ineffective and their use is restricted in or around public water supplies. Some managers are using floating machinery to remove cabomba, but these machines are expensive to purchase and operate and are restricted to areas of deep water and wide channels. In addition, they only remove the tops of the plants and the remaining stems soon grow back to the surface. It is likely that the only method that will be effective in reducing cabomba is biological control. This method involves introducing host-specific insects from the weed's country of origin. These herbivores feed specifically on the target plant and reduce the ability of the weed to outcompete other aquatic plant species. In 2003, CSIRO Entomology began a project to discover and test biological control agents from cabomba's native range in an effort to find a long-term sustainable solution to this problem. We have identified two insects, a weevil (*Hydrotimetes natans*: Curculionidae) and a moth (*Paracles* spp.: Arctiidae), that have potential for safe and effective control of cabomba. The weevil feeds internally on stem tissues as an immature and externally on foliage as an adult. The moth feeds externally on leaf tissue as an immature and does not damage cabomba as an adult.

There are three factors that primarily limit cabomba abundance in lakes and ponds. These are herbivores, competition from other plants (decreasing with water depth) and shade (increasing with water depth). Observations in its native range (herbivores present) indicate that the realised niche of cabomba is generally 2–4 m water depth. Lakes often have floating vegetation around the margins, which restricts cabomba from growing in shallow water. Cabomba rarely blocks whole water courses, forms dense patches or invades entire lakes, and is often found growing among other plant species. Dominance shifts from one species to another depending on the season, population age and climatic events. In the introduced range we find cabomba spanning a greater range of depths (from less than 1 m up to 6 m). Floating vegetation along lake or pond margins is rare, but competitive emergent vegetation is often dense at depths less than 1 m. In Australia, cabomba often creates dense monospecific stands that cover entire lakes. We hypothesise that in the absence of herbivores cabomba expands its realised niche. We predict that the addition of herbivores will lead to contraction of habitat and reduction in plant density to that observed in the native range (Fig. 1).

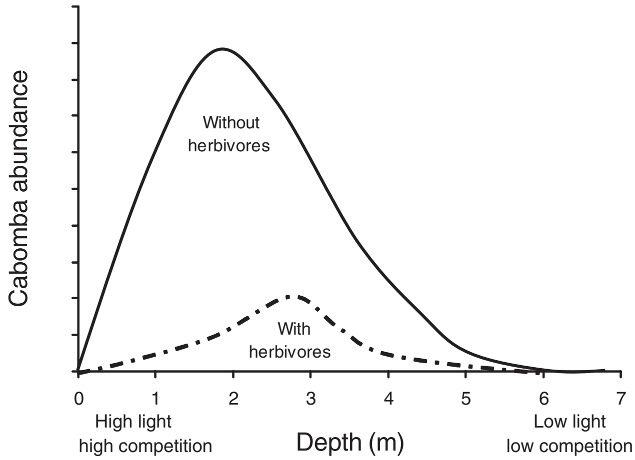

Fig. 1. Predictions of how cabomba abundance will change in the presence of herbivory. (i) Herbivores will decrease the competitive ability of cabomba, which will reduce abundance in shallow water where competition is most intense. (ii) Herbivores will reduce the ability of cabomba to tolerate deep water with low light availability and greater wave action. The result will be an overall reduction in abundance and a shift of maximum abundance to deeper water.

METHODS

We surveyed cabomba in three lakes in south-east Queensland over a 1-year period. These field sites were Lake Macdonald (−26.38549, 152.92905), Ewen Maddock Reservoir (−26.79658, 152.99017) and Siebs Dam (−26.49354, 152.97256). Samples were taken using a diving crew (SCUBA). Sampling was stratified by depth with 1 m increments from the deep water to shallow water (deepest sampling location was 7 m in Ewen Maddock). Three plots (0.25 m^2) were randomly located and all plants from within each plot were collected and brought to the surface at each depth. Plant material was taken back to Longpocket Laboratories (CSIRO Entomology, Indooroopilly) where stem length and number of plants were recorded. Material was then dried to constant weight (60°C) and weighed to the nearest 0.01 g. Samples were collected five times during the year to assess seasonal variation (September and November 2004; January, March and July 2005).

Cabomba populations were surveyed in the native range (Argentina, Uruguay, Paraguay and Brazil) to identify potential biological control agents. Surveys were primarily conducted by GC Walsh (United States Department of Agriculture-South American Biological Control Laboratory), but periodically assisted by M Julien and S Schooler. Two potential agents were found in the Corrientes province of Argentina: a weevil (*H. natans*: Curculionidae) and a moth (*Paracles* spp. Arctiidae).

Biomass data from Australia were quantitatively measured and biomass in Argentina was estimated based on observations. Conceptual estimate of effect of herbivory on plant abundance and distribution was based on knowledge of herbivore damage. For example, the stem-boring weevil is expected to weaken stems, which will likely reduce the ability of the plant to tolerant deeper water, while leaf defoliation by moth larvae is expected to have a greater impact on competitive ability in shallow water.

RESULTS AND DISCUSSION

We found that cabomba grew at depths up to 6 m (Figs 2–4). Native plants were generally restricted to depths of less than 2 m (primarily water snowflake, *Nymphoides indica*). We did not detect significant seasonal variation in cabomba plant population parameters over the course of the study (stem length, plant density or biomass). Therefore, we combined the seasonal data for each sample site. However, there was a strong response to water depth at all sites. In the following analysis we plot the mean values for the sites at each depth with associated standard error. We then predict the response of the population with the addition of the biological control agents.

Stem length

Stem length was positively correlated with water depth to a depth of 3 m, where plants averaged 272 cm in length (Fig. 2). The plant with the greatest stem length was 710 cm and was found growing in 4 m of water. We predict that weevil damage will weaken stems at all depths, but will more greatly affect longer stems. This will likely result in a greater decrease in stem length at greater depths as those plants will be exposed

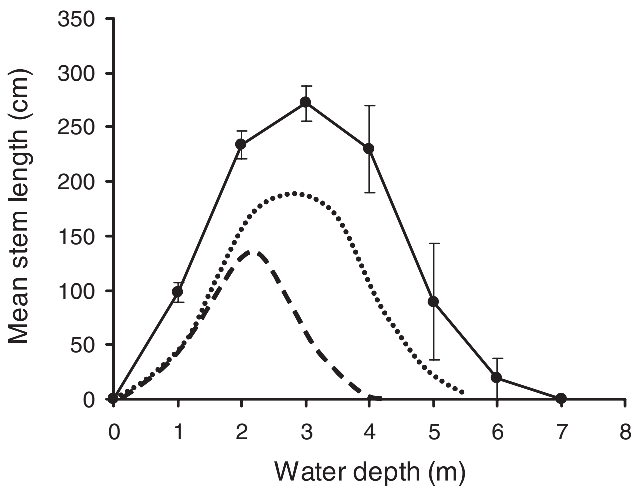

Fig. 2. Mean cabomba stem length is highly correlated with water depth to 3 m (solid line). We predict that stem-boring weevils (dashed line) will more greatly reduce stem length than leaf-feeding caterpillars (dotted line). Bars indicate the standard error.

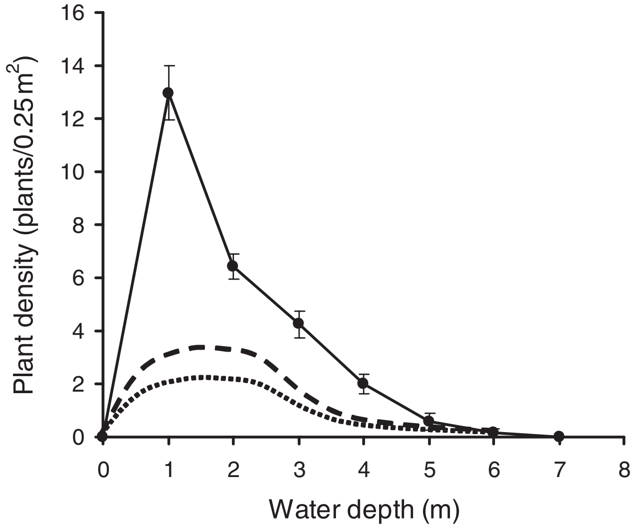

Fig. 3. Cabomba density decreases with increasing water depth (solid line). We predict that both agents will exert a greater impact on plant density in shallow water (where competition from other plants will increase the magnitude of the impact) and in deep water (where stress of reduced light will increase the negative effect of the herbivore damage). The leaf-feeding caterpillars (dotted line) are expected to have a greater impact than the stem-boring weevils (dashed line) because they directly reduce shading of cabomba in shallow water and reduce photosynthetic ability of cabomba in deeper water. Bars indicate the standard error.

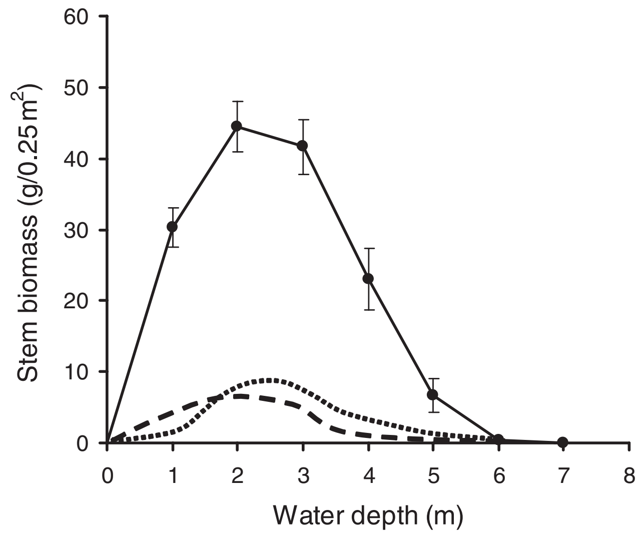

Fig. 4. Cabomba biomass exhibits a uni-modal distribution with increasing water depth (solid line). We predict that the defoliating moth (dotted line) will reduce biomass more than the weevil (dashed line) in shallow water due to increased light penetration favouring other plant species. The stem-boring weevils are expected to have a greater effect in deeper water due to weakening stems. Bars indicate the standard error.

to more physical stress. The moth will probably have a similar effect at all depths.

Plant density

Plant density was negatively associated with water depth. The mean number of plants per 0.25 m^2 decreased exponentially from 13 plants at 1 m to 0.2 plants at 6 m depth (Fig. 3). We predict that both agents will exert a greater impact on plant density in shallow water (where competition from other plants will increase the magnitude of the impact) and in deep water (where stress of reduced light will increase the negative effect of the herbivore damage). The leaf-feeding caterpillars are expected to have a greater impact than the stem-boring weevil because their leaf defoliation will directly reduce shading by cabomba in shallow water, thus increasing germination and growth of native plants. In deeper water the caterpillars will have a direct negative effect on the photosynthetic ability of cabomba.

Stem biomass

As expected from the relationship between stem length and density with water depth, stem biomass exhibits a uni-modal distribution with water depth with a maximum mean mass of 44.5 g/0.25 m^2 (dry weight) at 2 m depth followed by 41.6 g/ 0.25 m^2 at 3 m water depth (Fig. 4). We predict that the defoliating caterpillars will reduce biomass at shallow depths due to increased light penetration stimulating competition by other plant species. However, we expect that the stem-boring weevil will have less of an impact because a weekend stem is less likely to break in shallow water as it is in deeper water. In addition, stem fragments are likely to float to the margins and establish new plants. However, the weevil is likely to have a greater effect on biomass of cabomba in deep water as plants will no longer be able to maintain stem lengths that are adequate to intercept enough light to allow tissue maintenance and growth.

SUMMARY

We do not expect to accurately predict the magnitude of the effect of the biological control agents without additional experimental data. This would require either simulated herbivory experiments in the introduced range (which would be very difficult to conduct underwater in natural field conditions) or herbivore exclusion experiments in the native range (which are not possible due to the safety risk imposed by piranha and alligators). Laboratory experiments are possible, but would be unrealistic without the combined effects of competition at shallow depths and reduced light intensity and greater stress to stems at greater depths. However, we can hypothesise the relative effects of the two biological control agents given their differing modes of feeding and assumptions of how this damage will differently affect plants at increasing depths.

Observations of natural populations in Argentina suggest that cabomba is generally restricted to deeper water: (i) in areas of large lakes protected from high wave action (i.e. between floating vegetation islands as in Lago Iberá, Argentina); or (ii) in areas of smaller lakes along the edges of emergent or floating vegetation. This may be due to the combined effects of native herbivores' reducing competitive ability or weakening stem strength as we hypothesise above.

We predict that the different feeding modes of the herbivores will have differing impact on cabomba abundance and distribution if they are released in Australia. The stem-boring weevils are expected to have a greater impact in deep water and the defoliating caterpillars will have a greater impact in shallow water. These predictions are based on several assumptions: (i) that weevil stem damage will weaken cabomba stems; (ii) that stress on plant stems increases with depth; and (iii) that leaf removal will reduce the competitive ability of cabomba. We will examine these assumptions in future research. In addition, we will continue to monitor cabomba populations after the biological agents are released to determine whether these predictions are verified.

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